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Natural Variability of Specific Forest Insect Populations and Their Associated Effects in Colorado

J.M. Schmid and S.A. Mata

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Abstract

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The natural variability for specific native bark beetle (Coleoptera: Scolytidae) and defoliator (Lepidoptera: Lasiocampidae, Saturniidae, Tortricidae) populations in the forests of Colorado ranges from endemic to epidemic. The effects of endemic and epidemic populations of these species on the forest and related resources are contrasted. The frequency and duration of epidemics for each species are discussed. Most of these species are at endemic population levels or in the lower portion of their natural population range as of 1994. Frequency and magnitude of future epidemics are discussed.

Keywords: *Dendroctonus* beetles, western tent caterpillar, pandora moth, western spruce budworm

The Authors



J.M. Schmid (left) and S.A. Mata (right) joined the Rocky Mountain Forest and Range Experiment Station in the mid-1960s. Schmid worked on the mountain pine beetle and spruce beetle during the next 10 years while Mata worked with the other entomologists on the western spruce budworm and mountain pine beetle. In 1984, they were teamed together to investigate the relationship between stand density and mountain pine beetle-caused tree mortality. During the next 10 years, they produced a series of papers dealing with the mountain pine beetle, which included silvicultural prescriptions and a hazard rating plan for the beetle.

Cover photo: Tree mortality on the White River National Forest in the 1940s exemplifies the extreme effects of spruce beetle epidemics. Photographed in 1953 by N.D. Wygant.

Natural Variability of Specific Forest Insect Populations and Their Associated Effects in Colorado

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Natural Variability of Specific Forest Insect Populations and their associated effects in Colorado

J.M. Schmid and S.A. Mata

VARIABILITY OF FOREST INSECT POPULATIONS

The natural variability of forest insect populations is frequently needed in reports for forest plans because certain insects cause major disturbances in forests. They affect tree growth, stand structure, species composition, fire hazard, nutrient cycling, and decomposition of woody material. Although a multitude of insects dwell in Colorado forests, it is primarily specific bark beetles (Coleoptera: Scolytidae) and defoliators (Lepidoptera: Lasiocampidae, Saturniidae, Tortricidae) that significantly affect tree growth and survival and thus receive the most attention. The bark beetles are rarely seen because nearly all of their life is spent beneath host tree bark. However, their presence becomes evident when host trees discolor and die. Similarly, larvae of defoliator populations may be noticed descending from trees or crawling on the foliage; but it is usually the defoliation that catches the eye of the forest observer.

The natural variability for forest ecosystems has been variously defined. One current definition describes natural variability as the change in composition, structure, and function of an ecosystem over time as influenced by the frequency, magnitude, and pattern of disturbances (Iverson 1995). For forest insects, natural variability is essentially the variation in population numbers over time and space. Unfortunately, populations are rarely quantified in precise terms such as numbers per tree or numbers per land unit area. Instead, population levels are classified in relative categories such as endemic versus epidemic; or high, low, and moderate levels; or in terms of the amount of damage they cause such as the amount of defoliation or number of dead trees. Population levels thus classified are difficult to compare because these categories are imprecise and inherently variable. For example, a bark beetle population killing hundreds of trees ranging from 8 to 12 inches dbh

and a population killing hundreds of trees ranging from 12 to 16 inches dbh would both be classified as epidemic. However, the latter population would probably be much greater because more beetles would be required to kill the larger trees.

In this report, insect populations will be classified as endemic or epidemic. Endemic populations are low, relatively static numbers of an insect that cause essentially unnoticed or insignificant amounts of defoliation or tree killing in the forest (Graham and Knight 1965). Endemic populations represent the smallest population level. Epidemic populations are high, fluctuating numbers of an insect that cause readily noticed or significant amounts of defoliation or tree killing. In the epidemic phase, evidence of the insect population (defoliation, dead trees) is generally noticeable on a landscape scale but varies dramatically among stands within the landscape. Damage may be evident in just a few stands one year and then evident more extensively in those stands and in other stands the following year. Epidemic populations represent the largest population level.

Populations of forest insects vary spatially and temporally, i.e., from endemic to epidemic over time in a specific land unit and from endemic to epidemic among land units in a specific time period. For example, a particular bark beetle may be present in a stand with an average dbh >8 inches but absent from an adjacent stand of seedlings and saplings. Within the stand in which the bark beetle is present, the population may be <100 beetles this year and more than 1000 beetles next year. Because of flight ability, beetles may be essentially absent from a stand one year but number in the tens of thousands in that stand the following year.

A strict discussion of the natural variability of a particular insect would be limited to the spatial and temporal ranges in population numbers, i.e., the endemic and epidemic levels over time in given land units. Because such levels are imprecise, they can

only be discussed in general terms. Further, endemic and epidemic levels are less meaningful without additional knowledge of how their numbers influence the forest ecosystem. For example, what effect an endemic population of a 100 bark beetles has on the forest is entirely different than the effect of an epidemic population numbering 1,000,000 bark beetles. Therefore, this report will discuss the endemic and epidemic populations levels for specific insects, as well as the effects of these population levels on forests and related resources. In general, the bulk of this report is drawn from publications, notes, and unpublished reports dealing with populations within Colorado. Where information was lacking from that area, information is drawn from other parts of an insect's range such as Arizona or Idaho; so the reader should be aware that some information may be unconfirmed as characteristic of the insect within Colorado.

Mountain pine beetle (MPB)

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a native bark beetle (Coleoptera: Scolytidae) that attacks and infests primarily ponderosa pine (*Pinus ponderosa* Lawson) and lodgepole pine (*Pinus contorta* Douglas) in Colorado. In ponderosa pine, the MPB usually infests standing live trees >8 inches dbh but may attack trees <8 inches dbh when such trees are intermingled with larger trees (Sartwell and Stevens 1975). In lodgepole pine, the MPB attacks larger diameter trees but may also attack smaller trees when they are intermixed with the larger trees (Cole and Amman 1969). MPBs do not attack seedlings of either species but may attack ponderosa pine saplings when they are mixed with larger trees (see McCambridge et al. 1982b). During the initial stages of epidemics, trees are usually killed in small groups of 3-10 trees. As the population increases, such groups may coalesce into one large group of more than 100 dead trees. Endemic MPB populations are usually associated with single trees that are lightning-struck or diseased, cohabiting therein with other scolytids such as *Ips*.

The first trees attacked by the MPB become focus trees that attract subsequently emerging beetles. As MPB attacks fill the initial tree, later arrivals attack adjacent trees and thus create a group of infested trees. Large diameter trees are the primary focus

trees for the MPB in lodgepole pine (Cole and Amman 1969). Primary focus trees for the MPB in ponderosa pine are those with *Armillaria* infections, hit by lightning, damaged by wind, or attacked by a previous generation of MPBs (Eckberg et al. 1994).

The MPB influences stand structure in pure pine stands. The MPB kills greater proportions of large diameter trees (Cole and Amman 1969, McCambridge et al. 1982b), so the average stand diameter is lowered during epidemics. Depending on the extent of the tree killing within the stand, small to large openings may be created in the canopy. Soon after opening creation, herbaceous vegetation occupies the site in the absence of understory seedlings existing prior to the overstory mortality (McCambridge et al. 1982a). Mortality during extreme epidemics may kill the entire overstory, thereby converting the site to a younger age class of pine or to another seral stage.

Where pine and other tree species are mixed, the MPB influences species composition as well as stand structure (Amman 1977). In the absence of fire, MPB-killed lodgepole stands eventually succeed to Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] at lower elevations and to Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] at higher elevations (Amman 1977). If fires occur, they perpetuate the lodgepole in beetle-killed stands, and tend to eliminate Douglas-fir, subalpine fir, and Engelmann spruce (Amman 1977). MPB activity in ponderosa pine stands in Colorado may accelerate replacement by Douglas-fir on some sites.

MPB epidemics also influence herbage production, wildlife populations, and fire hazard. The growth of forbs, sedges, and grasses increases in beetle-killed spots (McCambridge et al. 1982a). Wild ungulates may benefit from the increased herbaceous production (Schmid and Amman 1992) and the standing beetle-killed trees may provide habitat for cavity-nesting birds. In general, the influence of MPB epidemics on animal species varies depending on the needs of the particular species (Schmid and Amman 1992). Fire hazard is increased for 2 years following MPB epidemics while the probability of higher-intensity fires may be increased for a number of years (Schmid and Amman 1992).

MPB populations have ranged from endemic to epidemic in ponderosa and lodgepole stands in Colorado. The frequency of MPB epidemics in a given area of lodgepole pine seems to range from 20 to 40

years depending on how rapidly some trees grow into large diameter categories (Amman 1977).

The frequency of MPB epidemics in ponderosa pine stands is somewhat ambiguous as exemplified by statements regarding the frequency rate for the Black Hills. Considering ponderosa pine stands in the Black Hills, Thompson (1975) cited seven epidemics over an 80-year period, which translates into an epidemic about every 11 years. Lessard (1986), apparently quoting Thompson's work, states MPB epidemics occur, on average, at 11-year intervals. However, Lessard's 11-year interval is misleading because in the latter portion of his text, the time periods for only five infestations are illustrated for the past 100 years, which equates to a MPB epidemic on 20-year intervals. More recently, Pasek (1992) indicated epidemics occur about every 20 years. Some of the ambiguity is created by imprecise definition of the beginning and end of epidemics. Thompson's report cites epidemics in 1962, 1967, and 1972, which implies three separate epidemics. These were not separate epidemics but part of a multi-year extensive epidemic in the northern Black Hills. If the three epidemics are considered one, then Thompson's data would show five epidemics over an 80-year period or an epidemic every 16 years. This situation exemplifies how the frequency rate for MPB epidemics may be different depending on how much area is considered and the amount of stand depletion by the previous epidemic (Schmid and Amman 1992). For a given stand, the frequency between epidemics may range from 50 to 100 years depending on how much of the original stand was beetle-killed (Schmid and Amman 1992). In the Front Range of Colorado, the last MPB epidemic ended in the mid-1970s so about 20 years have passed since that epidemic.

The duration of epidemics varies because unpredictable weather factors may cause rapid declines in MPB populations. In addition, the duration of epidemics may also be complicated by the area under consideration. An epidemic may last several years in a particular stand whereas the epidemic as part of a drainage may last for 10 or more years. Average duration of MPB epidemics in lodgepole pine is 6 years (Cole and Amman 1980) and generally less than 10 years (G.D. Amman 1992, personal observation). For ponderosa pine, short-lived MPB epidemics last 2-5 years and long-term epidemics last 7-14 years (see Blackman 1931, McCambridge et al. 1982b). The most recent MPB epidemic in the Black Hills

lasted 9 years (J.M. Schmid 1994, personal observation). The durations of MPB epidemics noted by Blackman (1931) and McCambridge et al. (1982b) were generally from epidemics after 1900 and, therefore, may have been unnatural durations because of increased stand densities resulting from fire suppression activities. However, data from Blackman (1931) suggest that a turn-of-the-century MPB epidemic lasted 14 years at a time when fire suppression activities had probably not influenced stand density. Therefore, the durations of more recent MPB epidemics are probably within the range of epidemic longevity.

MPB populations as of 1994 are at endemic levels in most National Forests of Colorado and are thus in the lower portion of their population range for this region. If current fire suppression policies are continued and silvicultural activities are minimized in the pine types for the MPB, stands will become more conducive for MPB epidemics.

Spruce beetle (SB)

The spruce beetle (*Dendroctonus rufipennis* Kirby) is a native bark beetle (Coleoptera: Scolytidae) that attacks and infests primarily Engelmann spruce in Colorado. The SB generally infests wind-thrown or downed trees (Schmid and Frye 1977). Endemic SB populations usually infest the lower sides of downed trees and may infest the upper surfaces if they are shaded. Individual standing trees may also be infested by endemic SB populations, but it is not known if such trees need to be predisposed by root diseases or physical factors.

Endemic SB populations develop to epidemic proportions in windthrown trees and then spread to standing trees when sufficient windthrown trees are not available to absorb the subsequent population (Schmid and Frye 1977, Holsten et al. 1991). Although most SB epidemics arise from windthrown trees, epidemics have been known to originate in logging residuals from right-of-way cuttings (Wygant and Lejeune 1967) and logging operations (McCambridge and Knight 1972). Epidemics are most common in overmature stands (>24-inch dbh) but may be sustained in large pole (8-inch to 12-inch dbh) and immature stands (Wygant and Lejeune 1967). SB may attack standing trees ranging from 4-inch to >30-inch dbh but rarely attack a tree <4-inch dbh.

During epidemics, standing trees of all sizes may be attacked but the SB prefers trees >20-inch dbh to trees of 6-inch to 8-inch dbh (Schmid and Frye 1977). Although the average diameter of attacked trees in some stands decreased as the White River epidemic progressed (Massey and Wygant 1954), it should not be implied that the SB always attacks the largest trees first and then proceeds to attack progressively smaller trees. Susceptibility of individual trees is influenced by more than just diameter so 12-inch or 16-inch dbh trees may be attacked first when intermixed with larger trees.

While susceptibility of individual trees of >12-inch dbh has not yet been precisely defined, relative susceptibility of spruce-fir stands to SB infestation can be determined. High hazard stands are those with: (1) average dbh >16 inches; (2) basal area >150 ft² per acre; (3) more than 65 percent spruce in the canopy; and (4) locations in well-drained creek bottoms (Schmid and Frye 1976).

Because endemic SB populations normally reside in windthrown spruce, they do not noticeably change stand structure and species composition. When endemic SB populations do infest standing trees, only single trees are usually infested so stand structure and species composition are negligibly changed.

In contrast, epidemic SB populations can drastically alter stand structure and species composition (Schmid and Frye 1977). During the White River SB epidemic in Colorado, epidemic populations reduced the average age of surviving trees, lowered the average diameter, average height, and the density, and left predominantly suppressed or intermediate trees as the only surviving spruce in many stands (Schmid and Frye 1977). This epidemic killed 99 percent of the overstory spruce throughout thousands of acres. Most SB epidemics do not reach the population magnitude and landscape proportions as the White River epidemic so their effects are not as extensive. For example, an epidemic in Arizona killed about 5 percent of the trees >5-inch dbh (Frye and Flake 1971). However, although epidemics are frequently of lesser magnitudes, their localized effects on stand structure may be just as severe.

When epidemic SB populations change stand structure, they also simultaneously alter species composition. Stands composed of 90 percent spruce and 10 percent fir in the overstory before the White River SB epidemic became 20 percent spruce and 80 percent fir after the epidemic (Schmid and Hinds 1974). In addition

to these relatively immediate changes in species composition, there are also long term effects on species composition. Under mature stands such as existed on the White River National Forest, fir seedlings greatly outnumbered spruce seedlings (Schmid and Hinds 1974). Such stands become predominantly fir as both species grow after release by the SB epidemic. They may remain predominantly fir for the next 125-175 years or until the fir begins to die (Schmid and Hinds 1974).

SB epidemics influence tree-water relationships such as interception and transpiration, and if the epidemic is large enough, streamflow. The death of overstory spruce greatly reduces interception of precipitation by the canopy and thus allows precipitation to reach the forest floor. Similarly, the death of overstory spruce also removes them as sources of transpiration for the ecosystem. If the SB epidemic reaches the size of the White River SB epidemic in Colorado, then streamflow can be affected. As a result of that epidemic, streamflow from the beetle-killed area increased 5.5-6.4 inches and streamflow for the entire watershed increased 1.6-1.9 inches (Mitchell and Love 1973).

Forage production in beetle-killed stands is much greater than in green stands. Grasses and sedges showed increased density in beetle-killed stands (Yeager and Riordan 1953). Forbs were 2.3 times more numerous in beetle-killed stands but browse plants decreased (Yeager and Riordan 1953). In general, the greatest density, number of species, and index of occurrence of plants were found in beetle-killed stands (Yeager and Riordan 1953). Although unmeasured, forage production probably increases each year following the death of the spruce and reaches maximum production in 3-5 years (P.O. Currie 1977, personal communication).

The influence of SB epidemics on animal populations inhabiting spruce-fir forests has not been determined but would depend on the species' requirements and the intensity and extensiveness of the epidemic (Schmid and Frye 1977). Hypothetical scenarios can be envisioned for some species with well-known habits or dependency on spruce. For example, insectivorous birds such as woodpeckers, nuthatches, and brown creepers (*Certhia americana* Bonparte) would initially benefit from the increased food supply and the availability of nesting sites (dead trees). However, as the insect populations declined from the loss of suitable hosts and emigra-

tion, these birds would also have to emigrate or decline in abundance. Seed-eating birds such as pine grosbeaks [*Pinicola enucleator* (Linnaeus)] and mammals such as red squirrels [*Tamiasciurus hudsonicus* (Erxleben)] are adversely affected immediately because of the loss of spruce seed (Yeager and Riordan 1953). In contrast, elk (*Cervus elaphus* Linnaeus) and mule deer (*Odocoileus hemionus* Rafinesque) benefit from the increased production of forage although the loss of the overstory cover may be detrimental.

SB epidemics can influence both fire hazard and fire intensity. Increased fire hazard (the probability of a fire starting) created by the killing of spruce by beetles is limited to the first 2 years after beetle attack when the dead and dying needles increase the fine fuel component. Once these fuels fall from the dead trees, fire hazard is essentially the same as before the trees were attacked by the SB. Although fire hazard should hypothetically increase during the 2 years following SB attack, the lack of fires following SB infestations suggests that fire hazard is not substantially increased. In contrast, fire intensity (the level of destructiveness of the fire if one starts) would increase after SB infestation and remain at a higher level for decades because of the increased dead fuel loads that don't readily decay. However, the probability for stand-replacement fires following SB epidemics appears to be negligibly increased by SB epidemics because such fires are so infrequent in spruce-fir forests (see Veblen et al. 1994).

The frequency of SB epidemics depends on the size of the area being considered, the extent of the SB-caused tree mortality and its' modification of stand structure in the stand(s) within this area, and how fast the stand grows into the hazardous condition (Schmid and Amman 1992). The frequency of epidemics in a particular stand is generally much less than that for an area composed of many susceptible and nonsusceptible stands. However, the epidemic frequency for that individual stand is also influenced by the extent to which a previous SB epidemic modified stand structure. For example, the White River SB epidemic in Colorado completely eliminated the susceptible-size spruce in many stands (Schmid and Frye 1977). Although the residual spruce (saplings, seedlings) in those stands could grow to become a susceptible stand in 80 to 100 years, the stands would be entering the lower threshold of susceptibility where the probability of an epidemic is low. It seems more likely that a higher level of susceptibility would

have to be reached before an epidemic would occur, i.e., a lower frequency or greater time interval between epidemics. In contrast, if the same stands suffered only limited mortality of susceptible-size trees because the epidemic collapsed before all the susceptible-size spruce were killed, then the stand could grow to a highly susceptible condition in less time. In that case, the time interval between epidemics could be shorter.

Within one area of ca. 8,645 acres on the White River National Forest in Colorado, three SB epidemics were evident since 1700 (Veblen et al. 1994). As determined from this data, the mean return interval for SB epidemics is 116.5 years and the turnover time is 259 years where mean return interval is the time interval between epidemics in a particular stand and turnover time is the time interval during which all the stands in an area are affected by epidemics (Veblen et al. 1994). Their mean return interval is a reasonable estimate for a single stand except that it may be greater if the stand was completely killed by a previous epidemic and less if the previous epidemic caused limited mortality (see Schmid and Hinds 1974).

SB populations as of 1994 are at endemic levels in the spruce-fir forests of Colorado. If silvicultural activities are minimized in the forest types for the SB, stands will become more conducive for SB epidemics.

Douglas-fir beetle (DFB)

The Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) is a native bark beetle (Coleoptera: Scolytidae) that attacks and infests Douglas-fir (Wood 1963). Endemic DFB populations in the Pacific Northwest and Idaho usually inhabit windthrown, physically damaged or diseased trees (Furniss and Carolin 1977) with attack densities greatest on the underside or shaded portions of windthrown trees (Furniss 1962). Endemic DFB populations in Colorado are presumed to infest these same types of debilitated trees but endemic populations have not been thoroughly studied. Mortality under these conditions in the Northwest may be substantial in total but widely scattered in Douglas-fir stands (Furniss and Carolin 1977).

DFB epidemics in the Pacific Northwest usually develop following extensive windthrow or fire (Furniss and Carolin 1977). In northern Idaho, epidemic DFB populations may have developed in trees

felled for reservoir construction and in snow-damaged trees in adjacent areas (Furniss et al. 1979). In contrast to Pacific Northwest populations, DFB epidemics in Colorado and Wyoming have arisen during and expanded following western spruce budworm (*Choristoneura occidentalis* Freeman) epidemics (Furniss 1940, Hester 1941, Hadley and Veblen 1993). Budworm defoliation apparently increases Douglas-fir susceptibility to DFB attack.

The DFB attacks standing trees with dbh ranging from 11-45 inches in southern Idaho (Furniss 1962); 10-29 inches in northern New Mexico (Chansler 1968); averaging more than 19 inches for 3 years in northwestern Wyoming (Pasek and Schaupp 1992); and 8-24 inches in northern Colorado (Lessard and Schmid 1990). Although Lessard and Schmid (1990) recorded attacked trees in the 8-inch to 11-inch dbh range, more trees were attacked in the 16-inch to 24-inch dbh range during the 1980s DFB epidemic (J.M. Schmid 1989, personal observation). This agrees with the results of Furniss et al. (1979), who found DFB kill larger dominant trees more frequently than smaller suppressed trees.

Tree mortality during epidemics ranges from scattered single trees to groups of 100 or more. Knight (1952) reported groups of 100-300 DFB-killed trees on the San Juan National Forest in southern Colorado but did not indicate the size of the land unit on which the groups were located. Hester's 1940 report indicates 21 and 38 infested trees per 640 acres on two surveyed areas in Wyoming, which suggests a more scattered distribution. Tree mortality during the 1980s epidemic in Colorado ranged from scattered trees to small groups and reflected the distribution of the susceptible-size trees (J.M. Schmid 1989, personal observation).

Beyond tree mortality, data are generally lacking with respect to the influence of DFB infestations on forage, big game and other animal populations, and water resources. Presumably, these effects would be similar but of a lesser magnitude than MPB or SB infestations.

The frequency of DFB epidemics is poorly understood in Colorado. Presettlement epidemics have not been uncovered. Epidemics occurred in 1934-1938, 1950-1951, and 1984-1990 in the Front Range of Colorado (DeLeon 1940, Hadley and Veblen 1993) so the interval between epidemics has ranged from 15-35 years. If DFB epidemics regularly follow WSBW epidemics, then epidemic frequency would be the

same as WSBW epidemics or at 20-year to 33-year intervals (see Swetnam and Lynch 1993).

The duration of DFB epidemics in Colorado is also poorly understood. Reports from the 1940s indicated DFB epidemics lasted 10 years in Wyoming (Hester 1941) and 5 years in Colorado (DeLeon 1940). Other reports (Furniss 1940, Knight 1952) indicate epidemics were in progress but did not specify their duration. A recent DFB epidemic persisted for 11 years (1982-1992) in the Front Range of Colorado (see O'Neil 1993).

The DFB epidemics of the 1930s were thought to be intensive but localized epidemics (DeLeon 1940), causing substantial tree mortality in a relatively small area. At the same time, epidemics occurred simultaneously in numerous locations in Colorado and Wyoming (see DeLeon 1940, Furniss 1940, Hester 1941), which suggests a synchrony of DFB epidemics on a larger scale. Inasmuch as Swetnam and Lynch (1993) have noted more synchronization of WSBW epidemics in the last 50 years, and DFB epidemics have coincided with WSBW epidemics, it appears that DFB epidemics during the past 60 years have been fairly synchronous in Colorado and Wyoming and perhaps more synchronous than in presettlement times.

DFB populations are generally endemic throughout Colorado. Epidemic DFB populations are declining in Northwestern Wyoming but still causing substantial mortality (see Forest Health Management Group 1994). Continued suppression of fires and cessation of silvicultural activities enhance conditions for WSBW epidemics and, therefore, coincidental DFB epidemics. However, the recent DFB epidemics killed a large proportion of the susceptible-sized Douglas-fir so the next DFB epidemics may not cause as much tree mortality in those areas.

Western tent caterpillar (WTC)

The western tent caterpillar [*Malacosoma californicum* (Packard)] is a native tent caterpillar (Lepidoptera: Lasiocampidae) that defoliates primarily aspen (*Populus tremuloides* Michaux) above 8,000 feet. This caterpillar also feeds on cottonwood (*Populus spp.*), willow (*Salix spp.*), and chokecherry (*Prunus virginiana* Linnaeus) at lower elevations in northern New Mexico (Stelzer 1968). WTC larvae consume aspen leaves in spring (Furniss and Carolin 1977). Leaves on trees of all sizes may be consumed when

the WTC is epidemic. The larvae may emigrate from completely defoliated trees and consume foliage on typically nonhost plants during the process.

Endemic and epidemic WTC populations cause disproportionate effects on individual aspen growth and survival. Endemic populations cause partial defoliation that probably results in negligible growth loss and rarely in tree death. The defoliation of one branch on an 8 inch dbh tree does not seriously reduce growth or cause death. In contrast, defoliation by epidemic WTC populations causes growth loss in defoliated trees; and complete defoliation for several consecutive years increases tree mortality. Complete defoliation for 1, 2, and 3 consecutive years reduced radial growth 28.4, 52.2, and 74.6 percent, respectively (Stelzer 1968). Over a 4-year period, percent tree mortality more than doubled on average, and percent top-kill more than tripled on average in three stands (Stelzer 1968). During the same period in three other stands, tree mortality remained below 34 percent and top-kill remained below 25 percent after 4 years (Stelzer 1968). Presumably, the differences in the percent tree mortality and percent top-kill in the two sets of stands reflect differences in the amount of defoliation suffered by the stands.

Stands in southern Colorado near LaVeta Pass suffered heavy mortality after 6 years of nearly complete defoliation from 1974 to 1980 (D.A. Leatherman 1995, personal communication). These stands were also infected with *Cytospora* and *Ceratocystis* cankers, which may have contributed to tree mortality (D.A. Leatherman 1995, personal communication).

Trees may refoliate after the first defoliation; but continued defoliation reduces the trees' capacity to refoliate in successive years. Complete defoliation for 1 year does not usually cause significant changes in stand structure. However, if defoliation causes the death of the overstory trees as described previously, then the stand may revert to an early age class, or in the presence of seedlings and saplings of a shade tolerant species such as white fir [*Abies concolor* (Gord. and Glend.) Lindl.] or subalpine fir, succeed to a spruce-fir stand.

The influence of epidemic WTC populations on big game, mammal and bird species inhabiting aspen forests, and water resources is unknown. Presumably, abundant WTC larval populations would benefit insectivorous birds such as cuckoos and vireos; and their populations would temporarily increase (D.A. Leatherman 1995, personal communication).

Complete defoliation for 1 or more years may reduce the amount of browse for mule deer and elk. If defoliation causes tree death, then this source of food is lost until aspen reinvades the area. Whether complete defoliation of aspen stands across a landscape or throughout a drainage causes changes in water yield such as that caused by the White River SB epidemic is unknown.

The influence of WTC populations on human activities is also not well quantified, but two observations reflect their nuisance value. Larvae and their frass dropping from trees in picnic grounds can annoy campers and picnickers. During one epidemic in northern New Mexico, emigrating larvae were so plentiful that their crushed bodies made the highway slippery on the Santa Fe National Forest (J.M. Schmid 1978, personal observation). Similarly, emigrating larvae caused trains of the Cumbres-Toltec railroad to slip on steep grades in southern Colorado (D.A. Leatherman 1995, personal communication).

The frequency of WTC epidemics in a specific stand is unknown. For the aspen forests of northern New Mexico and southern Colorado, epidemic frequency is between 10 and 20 years (see Stelzer 1968). The duration of an epidemic may exceed 10 years, but a recent epidemic on the San Juan National Forest lasted at least 9 years (see Raimo 1985). However, because a polyhedral virus can terminate the WTC epidemic quickly, the duration of an epidemic depends on how rapidly the virus spreads throughout the epidemic population.

WTC populations as of 1994 are at endemic levels in aspen forests in Colorado. Current knowledge suggests that stand structure does not influence the start of WTC epidemics so the lack of silvicultural activity and the continuation of fire suppression will not create stands more conducive to epidemics.

Pandora moth (PM)

The pandora moth (*Coloradia pandora* Blake) is a native moth (Lepidoptera: Saturniidae) that defoliates ponderosa and lodgepole pines in Colorado. The larvae eat needles on trees of all sizes. They generally consume needles 1 or more years old because most feeding occurs in the spring and early summer before the new growth flushes. Because the new growth is not usually eaten (Schmid and Bennett 1988), trees commonly have a flush of growth at the tips of the

branches the year they are defoliated. In addition, the PM has a 2-year life cycle, so most of the defoliation occurs every other year.

PM defoliation during epidemics reduces tree growth. Radial growth of defoliated trees in the North Kaibab (Arizona) epidemic was about 10 percent less than radial growth of undefoliated trees (Bennett et al. 1987). Growth of trees >14-inch dbh was reduced more than the growth of trees <14-inch dbh (Bennett et al. 1987). Basal area growth in the defoliated areas was about 15 percent less than basal area growth in undefoliated areas (Bennett et al. 1987). Based on these growth-loss estimates, defoliated stands lost 11 f.b.m. per acre per year (Bennett et al. 1987).

PM defoliation can cause tree mortality, but mortality may also be attributable to associated biotic agents. Although severe defoliation killed some trees during the first recorded PM epidemic in Oregon, most of the tree mortality resulted from subsequent bark beetle infestations (Patterson 1929). The death of lodgepole pine on southern exposures during a PM epidemic in Colorado was attributed solely to PM defoliation (Wygant 1941). During the North Kaibab epidemic, tree mortality was <1 percent throughout the affected area (Bennett et al. 1987). However, mortality was much greater in stands heavily infected by southwestern dwarf mistletoe [*Arceuthobium vaginatum* subsp. *cryptopdum* (Engelm.) Hawksworth and Wiens], especially when the heavily infected trees were severely defoliated two successive times (Wagner and Mathiasen 1985). Thus, while bark beetle epidemics have followed PM epidemics in some parts of the West (Furniss and Carolin 1977) because the PM defoliation apparently predisposed the trees to bark beetle infestation, this phenomenon is not universal. Bark beetle epidemics did not follow past PM epidemics in Colorado and Arizona (J.M. Schmid 1994, personal observation) nor have they followed the current epidemic in Oregon (B.E. Wickman 1995, personal observation).

The effects of PM epidemics on water, forage, and other resources has not been documented. Nutrients present in the foliage are added to the forest floor in the form of insect frass as a result of the defoliation. Defoliation of the dominant trees may expose the Kaibab squirrel (*Sciurus aberti kaibabensis* Merriam) to greater predation by the northern goshawk [*Accipiter gentilis* (Linnaeus)].

Time intervals between epidemics are estimated to be about 20 years in Oregon (Patterson 1929) and 20-30 years in other parts of the West (Furniss and Carolin 1977). In contrast, only one PM epidemic in Arizona and one in Colorado have affected more than 500 acres and lasted for several PM generations during the past 60 years. More recently, endemic populations have been noted in lodgepole pine stands in North Park about 75 miles west of Fort Collins, CO in 1984 (J.M. Schmid 1984, personal observation), and in ponderosa pine stands in the southern Black Hills (R. Dorsett 1994, personal communication, J.M. Schmid 1991, personal observation). However, these populations did not cause extensive defoliation over thousands of acres. Thus, the time interval between epidemics is at least 60 years for specific locations and, realistically, probably closer to 75-100 years.

Most PM epidemics last 6-8 years or 3-4 generations (Furniss and Carolin 1977). The North Kaibab epidemic had at least 4 generations of which three caused extensive defoliation and the final generation caused limited defoliation (Schmid and Bennett 1988).

PM populations as of 1994 are at endemic levels throughout Colorado. Current knowledge suggests that stand density and structure do not influence the start of PM epidemics so the lack of silvicultural activity and the continuation of fire suppression will not create stands more conducive to epidemics.

Western spruce budworm (WSBW)

The WSBW is a native moth (Lepidoptera: Tortricidae) that defoliates primarily Douglas-fir and white fir in Colorado. Less preferred hosts are Engelmann spruce and subalpine fir. WSBW larvae feed on cones, seeds, vegetative and reproductive buds, and foliage (Lynch and Swetnam 1992). The current year's foliage is usually consumed before older foliage is consumed. Foliage on trees of all sizes is consumed during epidemics. The feeding habits of endemic and epidemic populations are identical. However, larval numbers are so prodigious during epidemics that their simultaneous feeding on the various parts of the tree affects tree growth and survival whereas larval feeding by endemic populations has minute effect.

WSBW defoliation during epidemics reduces radial growth. Radial growth loss during four WSBW epidemics in one stand ranged from 0.13 to 0.43 inch

(Alfaro et al. 1982). Losses during the four epidemics equated to about a 1-inch loss in radial growth or 2-inch loss in diameter growth (Alfaro et al. 1982). This amounted to a 12 percent reduction in diameter growth over a 65-year period (Alfaro et al. 1982).

WSBW defoliation reduces height growth by top kill of recent previous growth, feeding on the terminal bud, and its resulting deformation of the main stem (Van Sickle et al. 1983). Height growth loss ranged from 16 percent to 21 percent after one epidemic and cumulative height loss after four epidemics was 32 percent (Van Sickle et al. 1983). Top killing in true firs (*Abies*) is greater than in Douglas-fir in mixed conifer stands (MacLean 1985). In mixed-conifer stands in northern New Mexico, understory trees <5-inch dbh suffered more crown damage than overstory trees >5-inch dbh (Klein and Bennett 1995).

Extensive WSBW defoliation for successive years causes tree mortality. Tree mortality can occur after 4 years of >40 percent defoliation per year and the number of dying trees increases dramatically with additional years of moderate defoliation (Alfaro et al. 1982). Suppressed and intermediate trees are killed more frequently than dominant and codominant trees (Alfaro et al. 1982, Klein and Bennett 1995). In mixed-conifer stands in the Blue Mountains of Oregon, WSBW-caused mortality has exceeded 85 percent in some stands and all crown classes have been killed (B.E. Wickman 1995, personal communication). After a 10-year epidemic in northern New Mexico, some stands lost more than 55 percent of their basal area and understory trees <5-inch dbh were killed more often than overstory trees >5-inch dbh (Klein and Bennett 1995).

Although WSBW defoliation alone can cause tree mortality, the defoliation may also indirectly kill trees by predisposing them to subsequent attack by DFB (see previous discussion for DFB). DFB populations caused substantial tree mortality in WSBW-defoliated Douglas-fir stands along the Front Range in Colorado during the 1980's (Johnson et al. 1989, Pasek and Angwin 1990).

WSBW epidemics alter stand structure. Epidemics in unmanaged multistoried stands may reduce the seedling and sapling component as well as suppressed and intermediate trees in the canopy (Carlson et al. 1983). If suppressed and intermediate trees are killed, average stand diameter increases while basal area decreases. In contrast, seedlings in managed stands are not significantly impaired because WSBW do not extensively feed on them (Carlson et al. 1983).

During epidemics, WSBW larvae may destroy cones and consume seeds (Dewey 1970). The percentage of budworm-damaged cones may vary from <10% to >90 percent depending on WSBW population levels (Dewey 1970). Cones may shrivel and die during early development because of budworm feeding or they may be hollowed during later development (Dewey 1970). In either case, seed loss is 100 percent. Budworm larvae do not always consume all the seeds in every damaged cone because some feeding is confined to the cone's surface; seed loss is restricted to only the feeding area (Dewey 1970).

Cone and seed losses may influence future regeneration under budworm-defoliated stands. Probability of achieving stocking on dry Douglas-fir sites was reduced about 30 percent when regeneration cuts were initiated during a WSBW epidemic (Carlson et al. 1983). Conversely, the probability of achieving stocking on moist Douglas-fir sites was not influenced by WSBW defoliation (Carlson et al. 1983).

WSBW epidemics may affect species composition and stand succession. Aspen stands with a white fir understory may revert to primarily aspen if WSBW defoliation causes death of the understory fir. Stands composed of ponderosa pine and Douglas-fir in the lower montane zone may revert to primarily ponderosa pine if a WSBW epidemic kills the Douglas-fir. However, predominantly Douglas-fir stands in the upper montane zone were retarded in their replacement of seral pine species by a WSBW epidemic but the epidemic did not reverse succession to the pine species (Hadley and Veblen 1993).

In turn, species composition may influence stand damage during epidemics. Mixed-conifer stands composed essentially of Douglas-fir and white fir suffered more damage than stands with Engelmann spruce five times more abundant than white fir (Klein and Bennett 1995).

The influence of WSBW defoliation on resources such as recreation, water quality, and cervine populations remains essentially undetermined. Although it is presumed that WSBW defoliation may influence recreation-use patterns of defoliated stands, this effect has not been clearly demonstrated (Bible 1985). Similarly, elk and deer populations may benefit from the increase in forage beneath defoliated stands as they apparently do in SB-killed stands; but the loss of hiding and thermal cover may be detrimental (B.E. Wickham 1995, personal communication). These positive and negative effects need confirmation.

HISTORICAL EVIDENCE AND FUTURE VARIABILITY

A number of avian and invertebrate species prey on different stages of the WSBW and thus are influenced by WSBW dynamics. Fourteen avian species including grosbeaks, juncos, sparrows, flycatchers, thrushes, and warblers are voracious predators of the WSBW (Langelier and Garton 1986). Some of these species functionally respond to epidemic WSBW populations (Torgersen and Campbell 1982) and thus benefit from the abundant food supply. Avian populations concentrate locally during WSBW epidemics (Takekawa et al. 1982); but whether concentrations represent a temporary increase by aggregation or a true increase in population numbers remains undetermined (Campbell 1993). In like manner, arachnid species of 11 families are associated with the WSBW in mixed-conifer stands in the Northwest and two families, the Salticidae and Philodromidae, are hunting spiders (Mason 1992) that should benefit from abundant WSBW populations. However, whether an increased functional response to WSBW populations also results in a numerical increase in arachnid populations remains unknown. Ants appear to be important predators of the WSBW (Campbell and Torgersen 1982) and exhibit spectacular functional and numerical responses to increasing WSBW densities (Campbell 1993).

The frequency of WSBW epidemics within the Colorado-New Mexico area varies from approximately 20 to 33 years (Swetnam and Lynch 1993) and frequency patterns have not changed measurably in the 20th century as compared to the 18th and 19th centuries (Swetnam and Lynch 1989). Individual stands may be subjected to an epidemic every 22-30 years (Lynch and Swetnam 1992). Duration of WSBW infestations in stands averages about 11 years (Swetnam and Lynch 1993), and epidemics may persist longer in older stands (Lynch and Swetnam 1992).

WSBW populations are generally at endemic levels throughout Colorado as of 1994. However, low-level epidemic populations seem to exist near Blue Mesa and Trout Creek reservoirs in Colorado (D.A. Leatherman 1995, personal communication). If current fire suppression policies are continued and silvicultural activities are minimized, stands will become more conducive for WSBW epidemics. Because multistoried stands provide more substrate for dispersing larvae than single storied stands (Wulf and Cates 1985), such stands enhance WSBW survival and the potential for epidemics.

Populations of the WSBW and SB reached epidemic proportions prior to 1875 or, in essence, before extensive settlement (see Swetnam and Lynch 1993, Veblen et al. 1994). Between 1875 and 1910, but as late as the 1940s for the SB³, populations of the MPB, SB, and WSBW reached epidemic status (see Graves 1899, Hopkins 1905, Schmid and Frye 1977, Swetnam and Lynch 1993). Although settler populations increased substantially during this period, fire suppression efforts in the respective forest types had not reached the point where the epidemics might be attributed in part to human prevention of natural forest fires. Thus, epidemics were part of the natural variation for MPB, SB, and WSBW populations before settlement and, probably, for DFB, WTC, and PM populations also.

Whether recent and/or current epidemics are outside the range or limits of presettlement epidemics remains questionable. As noted prior, epidemic is an imprecise term so comparing presettlement epidemics and more recent epidemics is difficult, especially when our knowledge of presettlement epidemics is so limited. In addition, "outside the range of variation" does not explicitly identify whether we are concerned with magnitude, frequency, or both.

Rather than debating whether current epidemics are different from presettlement epidemics, a series of more relevant questions needs to be addressed. Will insect epidemics be a part of future forests? Certainly, but it would depend on the species and the management of the forest involved. MPB, SB, and possibly DFB and WSBW epidemics could be prevented or minimized by good silviculture. Will epidemics be more frequent? Perhaps, but not necessarily. Wilderness and natural areas, parks, or any forested units where silvicultural activities are restricted or prohibited could experience MPB, SB, DFB, and WSBW epidemics at frequencies and magnitudes corresponding to presettlement epidemics. MPB, SB, DFB, and WSBW epidemics would be less frequent and damaging in forested areas where good silviculture is practiced. Could future epidemics cause changes in stand structure and density on a unit area

³I consider the White River SB epidemic of 1939-1951 to be essentially a presettlement epidemic.

basis (per acre) not evident during presettlement or recent epidemics? This seems unlikely because the gamut of stand changes has been experienced. Could future epidemics cause changes in stand structure and density on a landscape basis unparalleled by past epidemics? Yes, in some cases. Because of fire suppression, stand density and structure has changed significantly over the past 75 years, particularly in montane forests (Covington and Moore 1992). More recently, silvicultural activities in some National Forests have been reduced as management objectives and priorities have changed. This will also contribute to future increases in stand density and vertical structure. Such stand changes in pine and Douglas-fir forests throughout extensive areas creates highly hazardous conditions conducive for MPB, DFB, and WSBW epidemics over extensive areas. These conditions create the potential for epidemic magnitudes probably not present during presettlement epidemics. However, it should be remembered that epidemics have varying life spans. In order to exceed levels of tree mortality or defoliation evident in past epidemics, an epidemic would have to sustain itself for the maximum number of years.

REFERENCES

- Alfaro, R.I.; VanSickle, G.A.; Thomson, A.J.; Wegwitz, E. 1982. Tree mortality and radial growth loss caused by the western spruce budworm in a Douglas-fir stand in British Columbia. *Canadian Journal of Forest Research*. 12: 780-787.
- Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact on succession. In Mattson, W.J., ed. *Arthropods in forest ecosystems*. Proceedings in the Life Sciences. Springer-Verlag, Inc. New York, New York. p 3-18.
- Bennett, D.D.; Schmid, J.M.; Mata, S.A.; Edminster, C.B. 1987. Growth impact of the North Kaibab pandora moth outbreak. Res. Note RM-474. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.
- Bible, T.D. 1985. Economic considerations for spruce budworm management in North America. In Sanders, C.J.; Stark, R.W.; Mullins, E.J.; Murphy, J., eds. *Recent advances in spruce budworms research*. Proceedings of the CANUSA spruce budworms research symposium; 16-20 September 1984; Bangor, Maine. Ottawa, Ontario: Canadian Forestry Service. p. 176-187.
- Blackman, M.W. 1931. The Black Hills Beetle (*Dendroctonus ponderosae* Hopk.). Tech. Publication 36. Syracuse, NY: Bulletin of the New York State College of Forestry at Syracuse University. Vol. IV. No. 4. 97 p.
- Campbell, R.W. 1993. Population dynamics of the major North American needle-eating budworms. Res. Paper PNW-RP-463. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 222 p.
- Campbell, R.W.; Torgersen, T.R. 1982. Some effects of predaceous ants on western spruce budworm pupae in north-central Washington. *Environmental Entomology* 11: 111-114.
- Carlson, C.E.; Fellin, D.G.; Schmidt, W.C. 1983. The western spruce budworm in northern Rocky Mountain forests: A review of ecology, past insecticidal treatments and silvicultural practices. In O'Loughlin, J.; Pfister, R.D., eds. *Management of second-growth forests. The state of knowledge and research needs*. Proceedings of a symposium; 14 May 1982; Missoula, MT. Missoula, MT: Montana Forest and Conservation Experiment Station, School of Forestry, University of Montana. p. 76-103.
- Chansler, J.F. 1968. Douglas-fir beetle brood densities and infestation trends on a New Mexico study area. Res. Note RM-125. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.
- Cole, W.E.; Amman, G.D. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. Res. Note INT-95. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 7 p.
- Cole, W.E.; Amman, G.D. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part 1: Course of an infestation. Gen. Tech. Rept. INT-89. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 56 p.
- Covington, W.W.; Moore, M.M. 1992. Postsettlement changes in natural fire regimes: Implications for restoration of old-growth ponderosa pine forests. Proceedings of a workshop; 9-13 March 1992; Portal, AZ. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Gen. Tech. Rept. RM-213. p. 81-99.

- DeLeon, D. 1940. The Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins). Rough draft of a proposed pest leaflet on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 6 p.
- Dewey, J.E. 1970. Damage to Douglas-fir cones by *Choristoneura occidentalis*. *Journal of Economic Entomology* 63: 1804-1806.
- Eckberg, T.B.; Schmid, J.M.; Mata, S.A.; Lundquist, J.E. 1994. Primary focus trees for the mountain pine beetle in the Black Hills. Res. Note RM-531. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 10 p.
- Forest Health Management Group. 1994. Forest insect and disease conditions in the Rocky Mountain Region 1993. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources, Forest Health Management. 48 p.
- Frye, R.H.; Flake, H.W., Jr. 1971. Mt. Baldy spruce beetle biological evaluation—population trend, stand structure and tree resource losses. Fort Apache Indian Reservation, Arizona. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwest Region, State and Private Forestry, Forest Insect and Disease Management. 38 p.
- Furniss, M.M. 1962. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in Southern Idaho. *Journal of Economic Entomology* 55: 486-491.
- Furniss, M.M.; McGregor, M.D.; Foiles, M.W.; Partridge, A.D. 1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. Gen. Tech. Rept. INT-59. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 19 p.
- Furniss, R.L. 1940. Memorandum on examination of the Devil Mountain area, San Juan National Forest, Colorado. Memorandum on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 2 p.
- Furniss, R.L.; Carolin, V.M. 1977. Western forest insects. Miscellaneous Publication No. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.
- Graham, S.A.; Knight, F.B. 1965. Principles of Forest Entomology. McGraw-Hill Book Company. 4th Edition. 417 p.
- Graves, H.S. 1899. The Black Hills Forest Reserve. U.S. Department of Interior, Geological Survey Professional paper. The nineteenth annual report of the survey, 1897-1898. Part V, Forest Reserves. p. 67-164.
- Hadley, K.S.; Veblen, T.T. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Research* 23: 479-491.
- Hester, D.A. 1941. Extensive survey report of the Cody Canyon area, Shoshone National Forest, Wyoming, Fall of 1940. Unpublished report on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 6 p.
- Holsten, E.H.; Thier, R.W.; Schmid, J.M. 1991. The spruce beetle. Forest Insect and Disease Leaflet 127. Washington, DC: U.S. Department of Agriculture, Forest Service. 11 p.
- Hopkins, A.D. 1905. The Black Hills Beetle with further notes on its distribution, life history, and control. Bulletin No. 56. Washington, D.C.: U.S. Department of Agriculture, Bureau of Entomology. 24 p.
- Iverson, D. 1995. Framework for a shared approach to ecosystem management. Presentation at a U.S. Forest Service ecosystem management training session; 6-10 Feb. 1995; Prescott, AZ.
- Johnson, D.W.; O'Neil, C.G.; Haneman, D.M. 1989. Forest pest conditions in the Rocky Mountain Region 1988. Lakewood CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Timber, Forest Pest, and Cooperative Forestry Management. 33 p.
- Klein, W.; Bennett, D. 1995. Surveys to measure tree damage caused by a western spruce budworm outbreak on the Carson National Forest. 1984 and 1991. Biological Evaluation R3-95-1. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region, State and Private Forestry, Forest Health Management. 46 p.
- Knight, F.B. 1952. Unpublished results of a reconnaissance survey of the San Juan National Forest, Colorado, on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 3 p.
- Langelier, L.A.; Garton, E.O. 1986. Management guidelines for increasing populations of birds that feed on western spruce budworm. Agriculture Handbook No. 653. Washington, DC: U.S. Department of Agriculture, Forest Service, Cooperative State Research Service. 19 p.
- Lessard, G. 1986. Mountain pine beetle mortality in ponderosa pine Black Hills of South Dakota and

- Wyoming. Biological Evaluation R2-86-2. Lakewood, CO: U.S. Department of Agriculture. Forest Service, Timber, Forest Pest, and Cooperative Forestry Management, Rocky Mountain Region. 22 p.
- Lessard, E.D.; Schmid, J.M. 1990. Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in northern Colorado. *Great Basin Naturalist* 50: 333-338.
- Lynch, A.M.; Swetnam, T.W. 1992. Old-growth mixed conifer and western spruce budworm in the southern Rocky Mountains. *In* Kaufmann, M.R.; Moir, W.H.; Bassett, R.L., tech. eds. Old-growth forests in the Southwest and Rocky Mountain regions. Proceedings of a workshop; 9-13 March 1992; Portal, AZ. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Gen. Tech. Rept. RM-213. p 66-88.
- MacLean, D.A. 1985. Effects of spruce budworm outbreaks on forest growth and yield. *In* Sanders, C.J.; Stark, R.W.; Mullins, E.J.; Murphy, J., eds. Recent advances in spruce budworms research. Proceedings of the CANUSA spruce budworms research symposium; 16-20 September 1984; Bangor, Maine. Ottawa, Ontario: Canadian Forestry Service. p. 148-175.
- Mason, R.R. 1992. Populations of arboreal spiders (Araneae) on Douglas-firs and true firs in the interior Pacific Northwest. *Environmental Entomology* 21: 75-80.
- Massey, C.L.; Wygant, N.D. 1954. Biology and control of the Engelmann spruce beetle in Colorado. Circular No. 944. Washington, DC: U.S. Department of Agriculture. 35 p.
- McCambridge, W.F.; Knight, F.B. 1972. Factors affecting spruce beetles during a small outbreak. *Ecology* 53: 830-839.
- McCambridge, W.F.; Morris, M.J.; Edminster, C.B. 1982a. Herbage production under ponderosa pine killed by the mountain pine beetle in Colorado. Res. Note RM-416. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 3 p.
- McCambridge, W.F.; Hawksworth, F.G.; Edminster, C.B.; Laut, J.G. 1982b. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Res. Paper RM-235. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.
- Mitchell, M.E.; Love, L.D. 1973. An evaluation of a study on the effects on streamflow of the killing of spruce and pine by the Engelmann spruce beetle. Arizona Forestry Notes, Northern Arizona Univ. School of For. No. 9. 14 p.
- O'Neil, C.G. 1993. Forest pest conditions in the Rocky Mountain Region 1991. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Forest Health Management. 31 p.
- Pasek, J.E. 1992. Quotation in Beetle Mania, an article in the Rapid City Journal, March 21, 1992.
- Pasek, J.E.; Angwin, P.A. 1990. Forest pest conditions in the Rocky Mountain Region 1989. Lakewood CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Timber, Forest Pest, and Cooperative Forestry Management. 34 p.
- Pasek, J.E.; Schaupp, W.C., Jr. 1992. Populations of Douglas-fir beetle in green trees three years after the Clover Mist fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-92-01. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. 13 p.
- Patterson, J.E. 1929. The pandora moth, a periodic pest of western pine forests. Technical Bulletin No. 137. Washington, D.C.: U.S. Department of Agriculture. 20 p.
- Raimo, B.J. 1985. Western tent caterpillar: Blanco Basin, "V" Rock, Chama Basin areas, San Juan and Rio Grande National Forests. Biological Evaluation R2-85-7. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Timber, Forest Pest, and Cooperative Forestry Management. 9 p.
- Sartwell, C.; Stevens, R.E. 1975. Mountain pine beetle in ponderosa pine—prospects for silvicultural control in second-growth stands. *Journal of Forestry* 73: 136-140.
- Schmid, J.M.; Amman, G.D. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. *In* Kaufmann, M.R.; Moir, W.H.; Bassett, R.L., tech. eds. Old-growth forests in the Southwest and Rocky Mountain regions. Proceedings of a workshop; 9-13 March 1992; Portal, AZ. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. Gen. Tech. Rept. RM-213. p 51-59.
- Schmid, J.M.; Bennett, D.D. 1988. The North Kaibab pandora moth outbreak, 1978-1984. Gen. Tech. Rept. RM-153. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 18 p.

- Schmid J.M.; Frye, R.H. 1976. Stand ratings for spruce beetles. Res. Note RM-309. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.
- Schmid, J.M.; Frye, R.H. 1977. Spruce beetle in the Rockies. Gen. Tech. Rep. RM-49. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.
- Schmid, J.M.; Hinds, T.E. 1974. Development of spruce-fir stands following spruce beetle outbreaks. Res. Paper RM-131. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 16 p.
- Stelzer, M.J. 1968. The Great Basin tent caterpillar in New Mexico: Life history, parasites, disease, and defoliation. Res. Paper RM-39. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 16 p.
- Swetnam, T.W.; Lynch, A.M. 1989. A tree-ring reconstruction of western spruce budworm history in the Southern Rocky Mountains. *Forest Science* 35: 962-986.
- Swetnam, T.W.; Lynch, A.M. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63(4): 399-424.
- Takekawa, J.Y.; Garton, E.O.; Langelier, L.A. 1982. Biological control of forest insect outbreaks: The use of avian predators. *In* Trans. 47th North Amer. Wildf. and Nat. Res. Conf. p. 393-409.
- Thompson, R.G. 1975. Review of Mountain Pine beetle and other forest insects active in the Black Hills 1895 to 1974. Special Rep. R2-75-1. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Forest Pest Management. 33 p.
- Torgersen, T.R.; Campbell, R.W. 1982. Some effects of avian predators on the western spruce budworm in north central Washington. *Environmental Entomology* 11: 429-431.
- Van Sickle, G.A.; Alfaro, R.I.; Thomson, A.J. 1983. Douglas-fir height growth affected by western spruce budworm. *Canadian Journal of Forest Research* 13: 445-450.
- Veblen, T.T.; Hadley, K.S.; Nel, E.M.; Kitzberger, T.; Reid, M.; Villalba, R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain sub-alpine forest. *Journal of Ecology*. 82: 125-135.
- Wagner, M.R.; Mathiasen, R.L. 1985. Dwarf mistletoe-pandora moth interaction and its contribution to ponderosa pine mortality in Arizona. *Great Basin Naturalist* 45: 423-426.
- Wood, S.L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). *Great Basin Naturalist* 23: 1-117.
- Wulf, N.W.; Cates, R.G. 1985. Site and stand characteristics. *In* Brookes, M.H.; Colbert, J.J.; Mitchell, R.G.; Stark, R.W., tech. coordinators. Managing trees and stands susceptible to western spruce budworm. Technical Bulletin No. 1695. Washington, DC: U.S. Department of Agriculture, Forest Service, Cooperative State Research Service. p. 23-26.
- Wygant, N.D. 1941. An infestation of the pandora moth, *Coloradia pandora* Blake, in lodgepole pine in Colorado. *Journal of Economic Entomology* 34: 697-702.
- Wygant, N.D.; Lejeune, R.R. 1967. Engelmann spruce beetle *Dendroctonus obesus* (Mann.) (= *D. engelmanni* Hopk.). *In* Davidson, A.G.; Prentice, R.M., eds. Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Publication No. 1180. Ottawa, Canada: Canadian Department of Forestry and Rural Development. p. 93-95.
- Yeager, L.E.; Riordan, L.E. 1953. Effects of beetle-killed timber on range and wildlife in Colorado. *In* Trans. 18th North Am. Wildl. Conf. p. 596-616.



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Rocky
Mountains

Southwest

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of seven regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526